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EFFECTS OF LUMINANCE AND FLICKER ON OCULAR DOMINANCE  
SHIFT IN KITTEN VISUAL CORTEX(U) BROWN UNIV PROVIDENCE  
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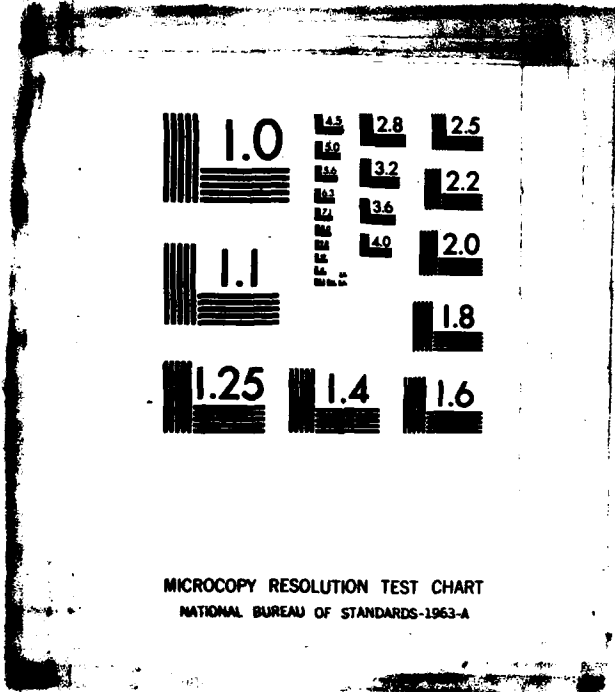
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We raised monocularly deprived kittens in visual environments with low level illumination that was either steady or flickering. With steady scotopic luminance ocular dominance shifted as it does in normal photopic lighting. In flickering light with an average frequency of 2Hz there was virtually no ocular dominance shift, while in flickering light averaging 0.1 Hz there was a significant shift. Recordings from the 2Hz flicker-reared are similar to the dark-reared recordings. The flickering illumination was produced in one case by a high contrast-low brightness TV near the cage, and in another case, by a low

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**Effects of Luminance and Flicker  
on Ocular Dominance Shift in Kitten Visual Cortex**

**by**

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### Summary

We raised monocularly deprived kittens in visual environments with low level illumination that was either steady or flickering. With steady scotopic luminance ocular dominance shifted as it does in normal photopic lighting. In flickering light with an average frequency of 2Hz there was virtually no ocular dominance shift, while in flickering light averaging 0.1 Hz there was a significant shift. Recordings from the 2Hz flicker-reared are similar to the dark-reared recordings. The flickering illumination was produced in one case by a high contrast -low brightness TV near the cage, and in another case, by a low voltage incandescent bulb driven by a pseudo-random sequence generator. This circuit delivered either a maximum ON time of 1.7 sec. or a maximum of 40 sec, for the 2Hz and 0.1 Hz respectively. Both the TV and flickering bulb produced average illumination comparable to the dim ( $0.01 \text{ cd/m}^2$ ) steady scotopic illumination. We conclude that dim flickering light is not a sufficient stimulus for promoting ocular dominance shift in kittens in the critical period unless the flicker rate approaches 0.1 Hz. Furthermore results from the TV rearing suggest that flicker may be capable of preventing an ocular dominance shift expected from a concurrent steady low light level background.

Key words: monocular deprivation. kitten visual cortex. scotopic vision.  
visual flicker. ocular dominance shift.

Single neuron studies in kitten visual cortex have provided neuroscientists with a systematic body of knowledge concerning the effects of environment on development (see reviews by Sherman and Spear, 1982; Movshon and Van Sluyters, 1981). In these studies the monocular deprivation (MD) paradigm has been particularly important. MD is closure of one eye during a critical period lasting from 3 weeks to 3 months of age, during which the normally binocular neurons of area 17 shift allegiance to the open eye (Wiesel & Hubel, 1963).

We are concerned with visual environmental factors which may affect ocular dominance (OD) plasticity. Other researchers have used restricted environments to study plasticity of monocular receptive field (RF) properties. For example:

- (i) Pettigrew & Freeman (1973) and Van Sluyters & Blakemore (1973) raised kittens in a planetarium environment.
- (ii) Cynader et al. (1973) and others studied the effects of strobe rearing.
- (iii) Hirsch & Spinelli (1970) examined the effects of stationary stripes of single orientation.

Studies such as these revealed rearing effects on orientation and direction selectivity. These authors sometimes reported OD histograms for their binocularly viewing kittens, but did not combine their unusual environments with MD.

There are two reports concerning restricted environments' effect on recovery from MD:

- (i) Daw et al. (1978) found that the OD shift expected after reverse suture at six weeks of age occurs even in kittens whose vision is limited to vertical stripes rotating at 30 deg/sec.

- (ii) Rauschecker & Singer (1979 & 1981) found that the expected reverse suture OD shift is incomplete if the second open eye views orientation more limited than the first open eye.

Our goal is systematically to study limited visual environments' effect on susceptibility to initial MD. We have begun our work by controlling the factors of luminance and rate of change of luminance (flicker). Our study is therefore of different emphasis from Blakemore (1976), who investigated the requirements for binocularity by varying the contrast, contour and correspondence of the two retinal images. We are concerned with luminance because as luminance decreases, visual function (contrast sensitivity, color, motion and depth perception) progressively declines. Perception of flicker, likewise, is a basic challenge to the visual system and its detection is influenced strongly by background luminance (Kaufman, 1974). We think these factors may be equally important during visual development. (See Aslin et al., 1981 for a general review.)

We reared kittens in a dark room in which we were able to control luminance. In "scotopic rearing" we placed a 75 watt incandescent bulb behind a translucent diffuser, 3m away from the kittens' cage. Driving the bulb with about 30v we were able to limit luminance of sawdust in the cage to  $0.01 \text{ cd/m}^2$ . The bulb was on continuously for 12 hr., then off for 12 hr. each day of conditioning. In "flicker rearings" we used the same 75 watt bulb, driven by 35v to achieve  $0.02 \text{ cd/m}^2$  in the cage, except that the circuit in Fig. 1 was used to pseudo-randomly turn the bulb off and on. ON and OFF time constants of the bulb are 500 ms and 125 ms respectively (1b). In one case, "ON" intervals ranged from 0.2 sec to 1.7 sec, averaging 2Hz in frequency, and in the other case from 5 sec to 40 sec, averaging 0.1 Hz. In both cases, total ON time was 40%. In "TV rearing" we placed a standard 48 cm black-and-white television set 50 cm from the front of the cage. We lowered the "brightness" control until the TV provided an average  $0.03 \text{ cd/m}^2$  luminance from the sawdust. "Contrast" was set to maximum, and a commercial channel tuned in so that, if a kitten choose to view the screen, it would see a series of flickering moving patterns. The source luminance of each small bright dot on the screen was about  $50 \text{ cd/m}^2$ . The TV provided both flicker and a relatively steady background of low luminance.



MD kittens reared in the home colony ("photopic") experienced 16 cd/m<sup>2</sup> average luminance of sawdust, on 12/12 hr. daily cycle.

Conventional single unit recording techniques (See Bear and Daniels, 1983) were employed to determine the ocular dominance and orientation selectivity of neurons in area 17 of cat visual cortex. Surgical preparation (and eyelid suturing) were performed with kittens anesthetized by ketamine and promazine (25mg/kg and 3mg/kg respectively). During recording, a gas mixture consisting of 75% N<sub>2</sub>O, 23% O<sub>2</sub> and 2% CO<sub>2</sub> was administered. The percentages of O<sub>2</sub> and CO<sub>2</sub> were adjusted to maintain end tidal CO<sub>2</sub> level between 3-4%, as monitored by an IR Industries Gas Analyzer. 12mg/kg/hr i.v. Flaxedil prevented unwanted eye movements. Intravenous Nembutal (2mg/kg) was used supplementarily if a strong paw pinch resulted in significant EEG changes or heart rate elevation. Two tungsten-in-glass electrodes simultaneously recorded single unit activities -one in the area 17 ipsilateral to the deprived eye, the other contralateral. We determined location of the areae centralis from the method of Olson & Freeman (1980). Recording continued for about 30 hrs after preparation, at which time the animal was sacrificed, and the positions of the electrodes were confirmed to be in area 17.

Table I summarizes the data base of 15 kittens and 813 units. Note that the onset of monocular visual experience varies from age 19 days to 40 days in the experimental series. All of these ages place the kittens well within the critical period for susceptibility to MD, especially considering that all were dark-reared from the age of 2 weeks until onset of visual experience.

Figure 2 shows the ocular dominance and selectivity histograms for the six groups. Six kittens which monocularly viewed low level, high contrast TV, or 1.7 sec flicker had virtually no ocular dominance shift in spite of an average of four weeks visual experience (2c,d). As Table I and Figure 2d show, the three kittens raised in 1.7 sec flicker had many NV (nonvisual units) and few selective cells--comparable to the dark reared sample of 2b. Four kittens which lived in scotopic light or very low rate

(40 sec max ON) flicker had nearly normal ocular dominance shifts, though the percentage of "selective" neurons was somewhat less than normal (2e,f).

Our results suggest that the ocular dominance shift expected after MD can be prevented by limiting the quality of the visual experience. We have shown here that intermittent dim, illumination of frequency 2 Hz is one such limited environment, but steady dim light, and slower flicker are not. The changing illumination of faster flicker presumably disrupts a stable view of the world in such a way as to impair image processing in visual cortex. We cannot expect that the LGN units providing cortical input were adversely affected - those units respond quite well to flashed stimuli (Daniels et al. 1978). The disruption must be intrinsic to neocortex. During development, minimum of 10 seconds of steady viewing may be necessary to promote a maturation process. Our results from the 0.1 Hz flicker support this conclusion.

In this regard we note that Blasdel & Pettigrew (1979) preserved binocularity in alternating-occlusion (AO) kittens by increasing the rate of alternation to greater than 0.1 Hz. Their data can be explained by our flicker results. In both cases, continuous stimulation through one eye for less than 10 seconds was insufficient to promote the OD shift common to AO and MD.

The closed eye lid reduces intensity and contrast (Sclar et al., 1983), but there may be just sufficient visual stimulation through the deprived eye (Spear et al. 1978) to influence binocular interaction. If a cortical adaptation to intensity or contrast change (Ohzawa et al. 1982) requires several seconds, then an intermittent stimulus may prevent sufficient adaptation to allow for binocular competition over the same dynamic range. This idea could be tested by excluding completely all visual stimulation through the closed eye (Hubel, pers. comm.).

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CAPTION

Table 1: Data summary: OD Shift index =  $\frac{R+RD}{\text{total units}}$ .

SEL (selectivity) index =  $\frac{SEL}{SEL+I+A}$ .

See Fig. 2 caption for definitions of variables.  
NV = non-visual.

The "TV", "flicker", "scotopic" and "darkrear" kittens were placed in the dark at about two weeks of age.

Note: K159 had corneal clouding of the left eye; no OD data was obtained.

Figure 1(a) Pseudo random sequence generator (PRSG)

By providing its own input through an exclusive -OR combination of its two most significant bit outputs the 8-bit shift register produces a repeatable sequence of 255 pseudo random bits . To insure that the circuit never collapses to zero output, all eight bits of shift reg. output are combined in a NOR gate (start-up circuit) whose output is "1" only if all eight inputs are "0". The pulse generator determines the rate of change of the output. For the "1.7 sec" flicker the generator was set at about 10Hz, for "40 sec" flicker the rate was 0.5Hz. The PRSG output controlled a noiseless relay in series with the line power to a Variac. The voltage on the Variac output determined the luminance of the lamp. Uniform lighting of a cage 3 meters away was insured by a translucent diffuser.

1(b) 2N5777 phototransistor output in the common emitter configuration, measuring light emitted from the incandescent 75 watt bulb. The bulb, at a voltage setting of 35V, has an ON time constant of 500 msec and an OFF time constant of 125 msec. The ON interval is 1.7 sec in duration in this figure.

1(c) Event histogram of the ON duration frequency for the circuit in (a). Total cycle time is 55 sec. Total ON time is approximately 40%.

Figure 2. Ocular dominance histograms and selectivity distributions for the six categories of kittens.

Ocular dominance: "B" represents units driven equally well by both eyes. "L" & "R" represent units driven exclusively by the left or right eye. Categories "BR" and "BL" represent units dominated by one eye but with a definite, mappable, field for the other eye. "RD" & "LD" are for units with very weak responses from the nondominant eye.

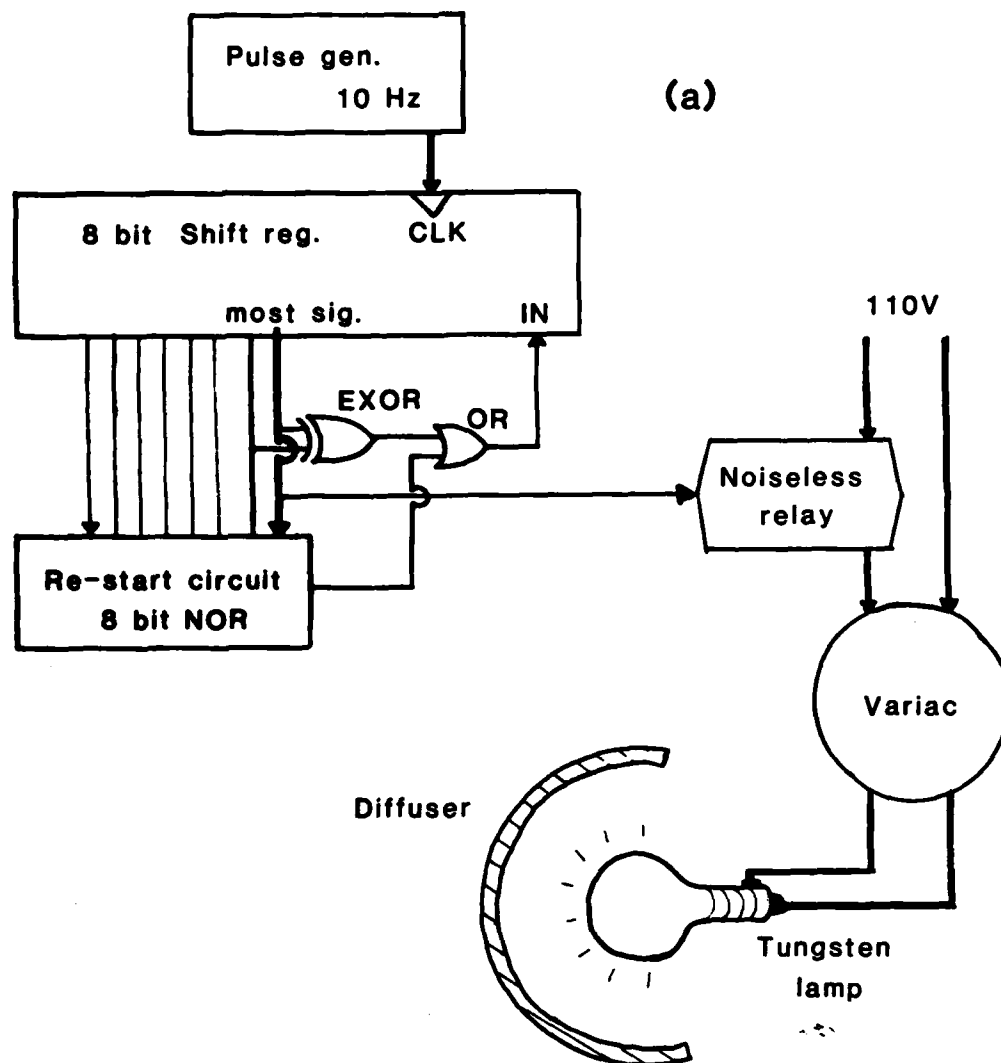
Selectivity: Cell classifications are similar to Buisseret & Imbert (1976). Aspecific "A" cells respond equally well to all orientations of moving stimuli. Immature "I" cells respond around the clock but have a factor-of-two preference for one orientation or axis. Selective "S" units have a null direction for which there is no response at all. Some cells were visually responsive but too sluggish to classify otherwise. They are in category "U" unclassified. All but the "dark reared" kittens had their left eyes closed before visual experience. Visual experience each day lasted 12 hours, followed by 12 hours of absolute darkness.

(a) Photopic. Normal artificial lighting; 16 cd/m<sup>2</sup>.

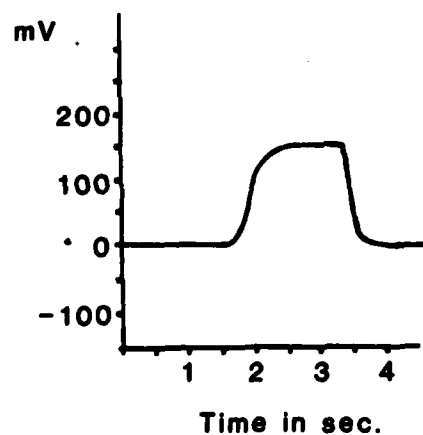
(b) Dark rearing. Absolute darkness in a two chambered ultra-flat black room.

(c) TV. 48cm standard black-and-white television was tuned to a commercial channel, the "contrast" set to maximum, and the "brightness" adjusted until a field of flickering dots was barely visible. The TV was placed 50cm from the front of the cage and was visible from virtually all parts of the cage. Brightness in the cage averaged about 0.03 cd/m<sup>2</sup>.

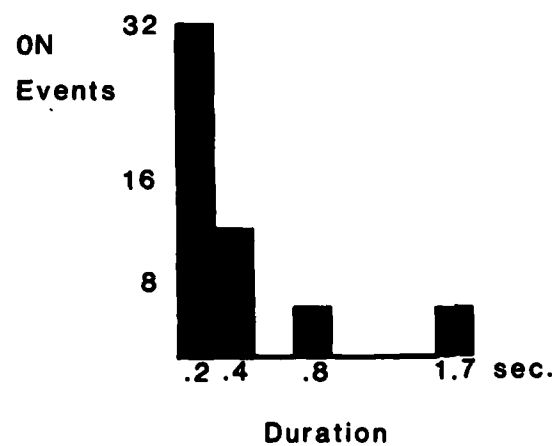
- (d) 1.7 sec Flicker. The circuit in Fig. 1 was used. The 75 Watt bulb's 1.7 voltage was set at about 35V to achieve an ON brightness in the cage of  $0.02 \text{ cd/m}^2$ . OFF was absolute darkness. Note that for the shortest duration ON, 215 msec, the bulb had achieved 65% full brightness, because of its 500 msec ON time constant.
- (e) 40s Flicker. The circuit in Fig. 1 was modified to have a clock rate 20 times slower than (d). All other conditions remained the same.
- (f) Scotopic. The same bulb-diffuser system from (d) & (e) was used with a voltage of about 30V, to achieve a steady brightness in the cage of  $0.01 \text{ cd/m}^2$ .



(b)

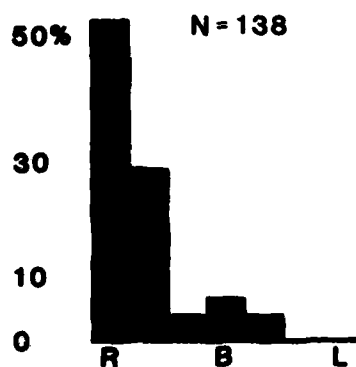


(c)

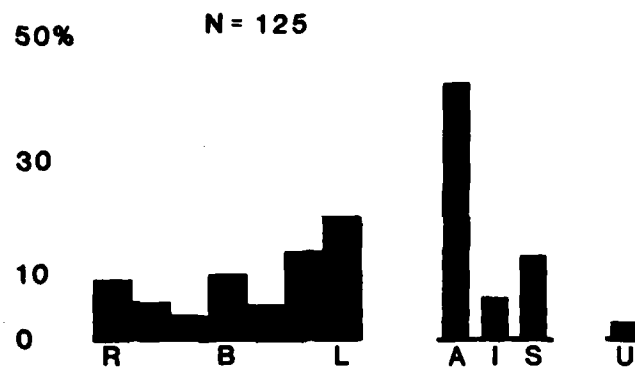




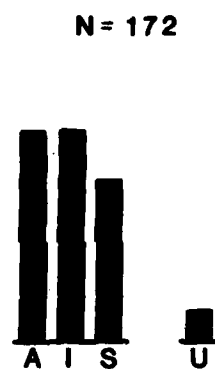
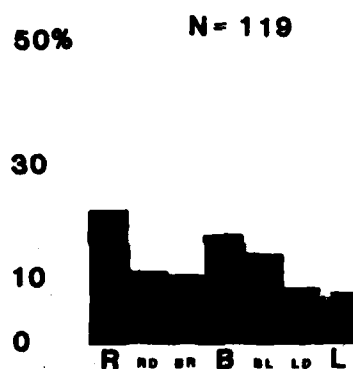
(a) Photopic



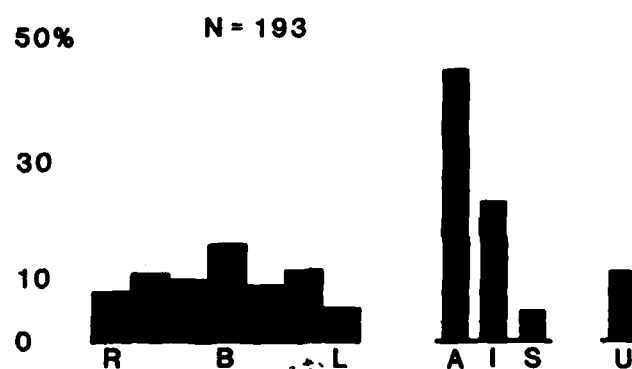
(b) Dark reared



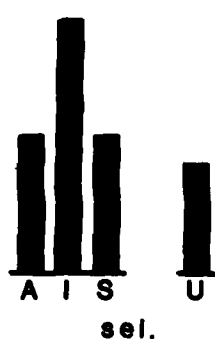
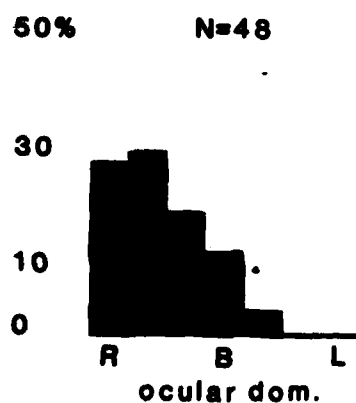
(c) TV



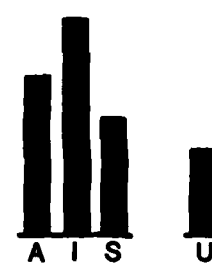
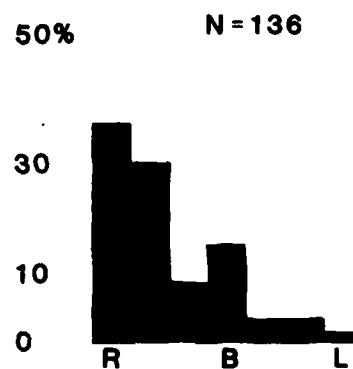
(d) 1.7 sec. Flicker



(e) 40sec. Flicker



(f) Scotopic



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